How Smart and How Social Is My Tiger Salamander?

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A 12 year old *Ambystoma mavortium melanostictum* male (from North Dakota) and a 3 year old *Ambystoma tigrinum* male (from Florida), who den together, in their feeding container. Companions of the author.

Study of Ambystomatid salamanders, the “mole” salamanders, is paradoxical. Axolotls, the aquatic Mexican Salamander, *Ambystoma mexicanum*, are relatively easy to keep and breed, so they have been used in embryology/ developmental biology research since the 1870’s. The ambystomatid salamanders are widely used in regeneration research as well: jaw, limb, tail, spinal cord, brain, jaw/teeth, thyroid, intestine and heart all regenerate. The tiger salamander, *Ambystoma tigrinum*, *mavortium* and relatives, has a classic neurobiology text written about it, “The brain of the tiger salamander” by C. Judson Herrick, published in1948 with 50 years of information compiled at that time. Ambystomatid salamanders are even used as disease models (Gross et al., 2002). But nothing about studying salamanders is easy.

It is difficult to study the natural behavior of most adult Ambystomatids. Except for mating season and dispersal of young salamanders to establish territories, few Ambystomatid salamanders go marching around in public during the day at any one time, making it hard to study them. Tiger salamanders, in particular, become tame so easily that laboratory studies of behavior are hard to accomplish. Try to sneak up on a tiger salamander in the lab to observe it and you are likely to find him (more males get captured at breeding or dispersing season) staring back at you in a state of hopeful expectation of being fed (conversation with Peter Ducey in the late 1990’s). In captivity they frequently initiate interactive behavior to reinforce the feeding and social bond. They spring at you, shoot out their tongues, stand up and scrabble at the side of their terrarium and knock on the side with their head, making them hard to ignore. (Though the head knocking can look alarming, the impact is cushioned by the auditory system-related milky fluid-filled endolymphatic sacs that wrap over the brain. Structure described in “The brain of the tiger salamander”.).

There is a literature on Ambystomatid behavior that provides insight into the tame behavior that develops easily in captivity for many species. If a tiger salamander keeper has ever wondered “how smart are they?” or “why do they adapt to captivity so well?”or “what behavioral stages do they go through” or “why on earth are they doing that?” the scientific behavioral literature and field studies provide some hints.

My interest in axolotls in the lab and tiger salamanders as pets made me curious as to the source of their engaging behavior in captivity (Chernoff, 1999a,b, 2000, 2001, available on my www.researchgate.net page). The 2000 article reviews the scientific ambystomatid behavior literature to that point. I would like to explore just two points here: salamander intelligence/learning ability and the degree to which they are social. Some of what follows is literature review and some is personal observation from 20+ years of salamander keeping.

How smart is my tiger salamander?

There are two types of studies that provide insight into Ambystomatid intelligence: counting and learning experiments. In general the numbers of metamorphosed juvenile or adult tiger salamanders used is small (5-19 per experiment).

Counting. There are studies on salamander “numerosity”, sensing of different quantities. These are not performed with tiger salamanders. Because they are small, easily kept in small containers and territorial, redback salamanders, the Plethodontid (lungless) salamander *Plethodon cinereus* has a substantial behavioral literature. In counting studies a majority of individuals (20 vs 10) choose tubes of 3 fruit flies vs tubes with 2 fruit flies (Uller et al., 2003). A study with 2 other

Plethodon species (*P. shermani*, and *P.metcalfi*) examined their ability to detect a larger amount of crickets based on ratios (Krusche et al., 2010). The salamanders preferred larger numbers of live crickets when the ratio was 1:2, but could not deal with 2:3. Similar studies with Ambystomatids do not exist.

Personal observation with tiger salamander "counting". If it isn't "stuff me full of food, Summer is ending" season, pet tigers will learn how many servings of food they get. All but one of my pet tigers has preferentially taken its food from forceps. Place the food in front of them, and they'll often ignore it for quite some time while continuing to beg. If they are getting one large cricket for a period of time (≥week), they will grab their cricket from forceps then back away into their shelter. If switched to two servings of smaller crickets they get very excited. Go the other way and a food riot may occur when the additional food item is not forthcoming. More than three servings make them very excited, as though they expect ALL the crickets and they take a considerable time to calm down. My observations over the last 20+ years are merely anecdotal, but I wonder if they sense the number of "food events": one, two or three events. Is this a form of response learning? The scientific salamander counting studies are never done by offering single food items in series.

Learning ability, mazes. Amphibians have traditionally been viewed as acting on instinct, but they do actually learn like higher vertebrates in some respects. In learning studies tiger salamanders have been subjected successfully to classical conditioning (learning to respond to a non-painful stimulus in place of a training shock), producing a skin electrical potential change in response to olfactory stimuli (Dorries et al., 1997). Tiger salamanders learn instrumental approach behavior (a type of conditioning): they were trained to snap at a manually manipulated target to get a food reward, a procedure which they forget over time without the stimulus (Davis and Singer 1967). Instrumental avoidance behavior (another type of conditioning) was shown when tiger salamander learned to avoid a bright light, cued by a vibration in advance of the light or an olfactory agent (Ray 1970; Mason et al., 1980).

Larval and adult tiger salamanders have been tested for position discrimination in T-shaped, simple mazes (Figure 1). In one study larval tiger salamanders were trained to run through a "water deprived" maze to get to a container of water, then were tested again as metamorphs. Another 10 were trained to run the maze only as metamorphosed animals. They reported that those trained as larvae re-learned the maze faster when tested after metamorphosis (Schwartz and Cogan, 1977). More recently, the T-maze study of Kundey et al., (2016) showed that the salamanders learned what turn to make, but failed to learn to follow visual cues indicating which turn to make. So they are not as smart as a rat.

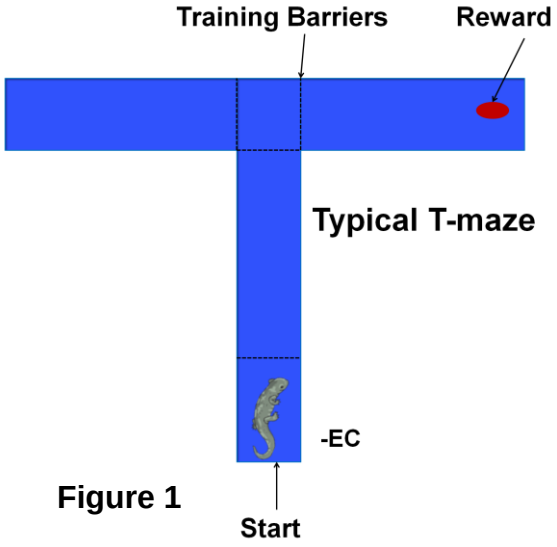


Figure 1

Does my tiger salamander like to socialize?

Tiger salamanders tame easily and are very interactive with their keepers, but is this behavior reflected in social interactions in nature? Larvae group together in a pond. Juveniles and adults are described as denning together in times of drought to conserve body water (Gehlbach et al., 1969). Adults have traditionally been described as solitary outside of mating season, but there is a literature

that suggests that they can be, to some degree, social with members of their own species and small mammals in nature. Some migration tracking studies have revealed examples of tiger salamander burrow sharing with conspecifics (Titus et al., 2014). Numerous videos exist showing multiple tiger salamanders entering a common burrow or burrow system and make interesting viewing. I recommend: https://www.youtube.com/watch?v=rJQ6M1vgOiA
(-in Colorado, posted 2012 by Smetlogik, recorded 2011, multiple salamanders starting around 48 seconds). They certainly adjust to living together in captivity and some are calmer and eat better when living with a companion (Figure 2. in each, left to right: A male, female; B male, male; C female, male, male).

Denning Together

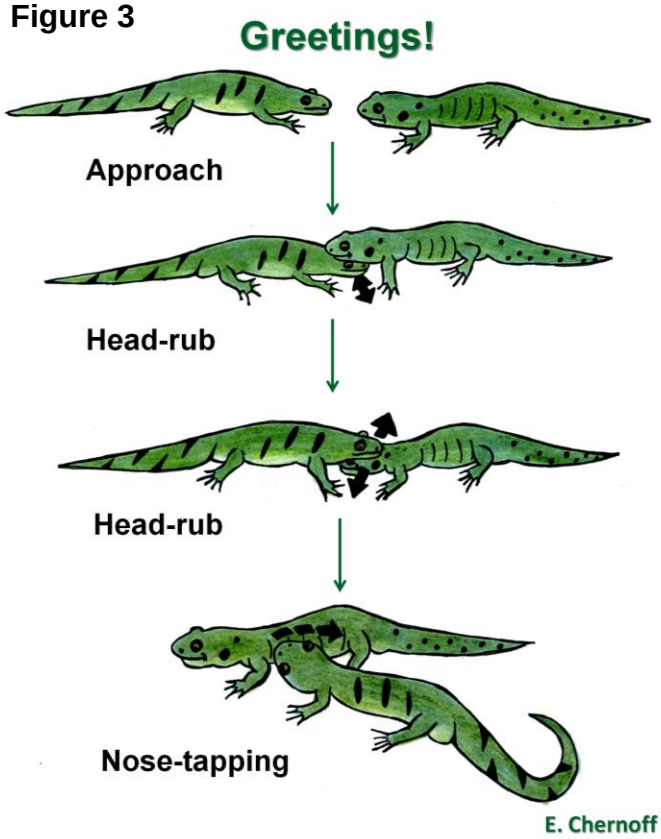
Adult mavortium. Watching the camera near their shelter. Relaxed

Adult melanostictum, young adult tigrinum. Watching from their shelter. Relaxed

Jammed themselves together during photo session. Stressed

Figure 2

Figure 3



Adult animals of both sexes, tigrinum and mavortium, will perform this greeting when introduced in a large bowl (neutral territory). Over time it decreases to a few nose taps or a brief head rub. Long term companions seldom greet.

Aggressive behavior. In captivity, I have seen juveniles challenge each other and challenge adults when first introduced. They usually make visual displays without biting. The tiger salamander dominance gesture has been described in experimental observations in Ambystomatids (Ducey and Ritsema, 1988; Ducey, 1989): forelimbs are extended fully and the head raised to display the throat and chest to the other salamander (Forebody elevation, head level (forebody raised on forelimbs, head and neck at 45° angle, Ducey, 1989). An agonistic (confrontational) interaction can be diffused if one of the participants performs a “look-away” or “turn-away” (individual facing opponent turns head or forebody away, holds position. then back). This also works when a less than 1 ounce (<28 gm) juvenile tiger salamander is challenging its human with a dominance gesture. A look-away performed by the human, makes the salamander friendlier and calmer and stops the challenges. I am amazed by how effective this is.

Biting, when it occurs, is usually once on the snout in food disputes. They will pull food items out of each other's jaws if you don't feed the feistier animal first. There is also often a "bitey stage" when they enthusiastically attack the fingers of the "feeds me" human. Experimentally, an abundance of food reduces aggression between ambystomatids (Ducey and Heuer, 1991). It doesn't stop tiger salamanders of all ages from what appears to be sniffing each other's breath at feeding time, however (personal observation).

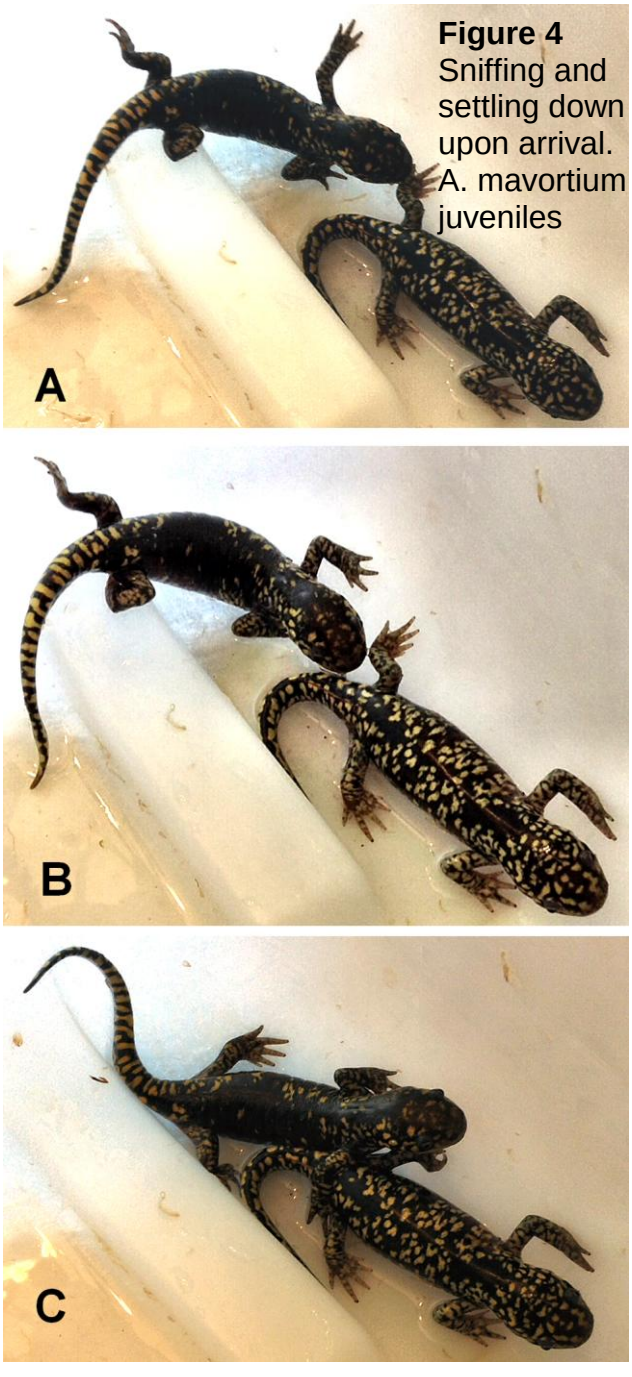


Figure 4 Sniffing and settling down upon arrival. A. mavortium juveniles

"Greeting" and association. Over the years I have observed newly introduced pet tiger salamanders (*tigrinum* and *mavortium* subspecies) engage in a process that looks like a formal greeting (Figure 3). As time goes by they develop a shorthand version. This "greeting" is almost always a peaceful process. The new introduction and "greeting" behavior of young metamorphs often seems less organized/stereotypical (Figure 4,5), but may reflect agitation due to shipping or association/co-housing prior to shipping. There is a lot of sniffing of each other (Figure 4) and of human fingers. Animals that I have raised through metamorphosis perform the full greeting. Only once have I observed a formal "greeting" associated with aggression between salamanders: a male juvenile Western/Barred tiger being introduced to an adult female performed the greeting then bit the adult on the snout and hung on. Twice, before I could stop it. The adult grabbed the juvenile by the arm and shook him hard. Both times. The next year, to calm his frantic attempts to escape during his first mating season, I put them together and they became terrarium buddies for 14 years, curling up under the same shelter or in the same burrow.

Without exception, after becoming tame, my pets will climb up my shirt and nose tap my chin. Some also rub their head under my chin. They do this when young and after emerging from a period of sleep as adults. Interacting with their "feeds me" may not be solely based on maintaining a food supply: in nature they interact with other mammals. Some ambystomatids, including tiger salamanders of various species and subspecies have also been found to cohabit with small mammals. Many types of rodent burrows are used by *A. marvortium mavortium* (Western or Barred tiger) and subspecies, *A. tigrinum* (Eastern) and *A. californiense* (California tiger) and *A tigrinum stebbinsi* (Sonoran tiger salamander). The best-known examples are the presence of tiger salamanders in burrows in prairie dog towns with black-tailed prairie dogs (*Cynomys ludovicianus*, reviewed in Shipley et al., 2006; Kretzer and Cully,

2001), where tiger salamanders are often among a variety of small vertebrates sharing prairie dog burrows. The range of mammalian burrows used by tiger salamanders of all kinds includes prairie dogs, pocket gophers, ground squirrels, pocket mice and deer mice (Shipley et al., 2006; Hickman, 1977; Semonsen 1998; Loredo et al., 1996; Richardson et al., 2000). Tiger salamanders need to den deep in the earth to avoid dry, hot summers or cold winters, so it is not surprising that they will occupy abandoned mammalian burrows (Figure 6).

The cases in which they have been shown to cohabit/associate with the resident mammals are more interesting. The paper that first brought this phenomenon to my attention was Semonsen, 1998, in which multiple California tiger salamanders (*A. californiense*) were found hibernating with a ground squirrel. They were not only in the same burrow chamber, but some salamanders were found to be under the ground squirrel when light associated with the fiberoptic system used to examine the burrow woke the squirrel. Another type of interaction between a small mammal, a resident pocket gopher (family Geomyidae), and an associated tiger salamander is described in Hickman 1977: "[the pocket gopher was] at the end of a tunnel, apparently to begin excavating, only to find a tiger salamander at rest. The pocket gopher picked the

Photo of a California tiger salamander (*A. californiense*) entering a small mammal burrow The photos of the CTS originally shared with Calherps are from Melissa Newman when volunteering in Chris Searcy PhD research project at UC Davis at Jepson Prairie. Used with permission. Melissa Newman is currently Program Coordinator of River Restoration and Invasives for Benton Soil and Water Conservation District in Corvallis OR.

salamander up by the mid-dorsal skin with the incisors, turned, and deposited the animate obstruction 0.6m away from the plug. The pocket gopher then returned to the plug to begin excavating. The salamander did not appear agitated or physically harmed. (Hickman 1977, p 237)". The salamander is identified as *A. tigrinum*, but this was before reclassification of tiger salamanders in the late 1990s (Irschick and Shaffer, 1997). Larger scale experimental studies (Loredo et al., 1996) reported juvenile and adult California tiger salamanders in occupied ground squirrel burrows. Of 57 burrows included in the study, 68% were "unambiguously occupied" by ground squirrels (fresh digging and feces at entrance) and salamanders (trapped, then followed to their burrows).

An infrared image video clip can be viewed free, though not shared in publication, that shows a tiger salamander in a burrow with a deer mouse (probably *Peromyscus maniculatus*) in South Dakota. The salamander does not seem to mind being stepped on (stop video progress with mouse clicks to see details: https://www.videoblocks.com/video/tiger-salamander-spring-night-burrow-underground-infrared-42tqng7ux/. Do tiger salamanders cohabiting with small mammals try to greet them? Prairie dogs "kiss" each other. Do they kiss their salamanders?

Eastern tiger salamanders (*A. tigrinum*) do also dig their own burrows in nature, at least for short-term use (Madison and Farrand, 1998), The excavation prowess of tiger salamanders has been studied in the lab (Semlitsch 1983) and can be confirmed by any keeper who has watched these pocket rototillers destroy terrarium landscaping. The video link indicated here shows one digging: https://www.youtube.com/watch?v=JqOwTL4Jbcg (Tiger salamander digging its own burrow in a mole hill, 2014, posted by Kalvin Knaggs, Manitoba Canada). Even when digging on their own, they are said to dig mainly in disturbed soil (no claws), often in ground loosened by burrowing mammals as in the video, so mammal burrows are very important to tiger salamander habitat,

Denning with mammals may be an ancient practice for amphibians (Fernandez et al., 2013). In 2013, imaging was performed on an unusual fossil from the Early (Lower) Triassic period, about 250 million years ago. It was found in South Africa, which was part of Gondwanaland in the Early Triassic. A preserved burrow was found to contain a fossilized, injured (wound holes in skull) Temnospondyl amphibian (*Broomistega*, upside down, green arrow) curled up alongside an apparently estivating therapsid mammal forerunner (*Thrinaxodon*, brown arrow; Figure 7). The injured amphibian may simply have taken refuge with a sleeping mammal forebearer, and Temnospondyl amphibians are not salamanders. The earliest known salamander fossils date to the middle Jurassic (≤170 million years ago) though their diversity suggests an earlier origin, and the relationship of caudata/urodela to Temnospondyls is still debated (157 million years ago in Anderson et al., 2008; Averianov et al., 2008; Gao and Shubin, 2012). Fossil *Ambystoma* closely related to the *tigrinum* group, *mexicanum* group fossils, only date back to the Late Miocene (11.6 million to 5.3 million years ago; Holman

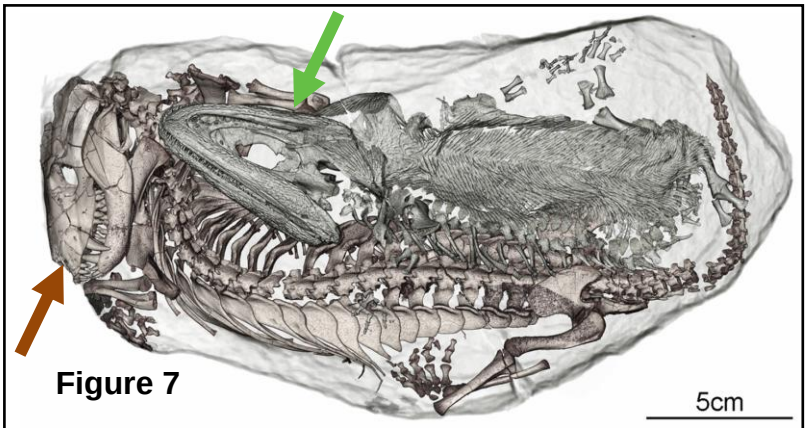


Figure 7

By Vincent Fernandez, Fernando Abdala, Kristian J. Carlson, Della Collins Cook, Bruce S. Rubidge, Adam Yates, Paul Tafforeau [CC BY 2.5] (http://creativecommons.org/licenses/by/2.5)], via Wikimedia Commons

2006). But it does make me wonder whether salamander/mammalian association has ancestral roots or is something amphibians and mammals have developed independently on multiple occasions.

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